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Resting cells of microorganisms in the 20–100 μm fraction of marine sediments in an Antarctic coastal area

Mutsuo Ichinomiya [a,*], Miwa Nakamachi [b], Mitsuo Fukuchi [c], Akira Taniguchi [d]

[a] *Laboratory of Aquatic Science and Consultant, Kamiikedai, Tokyo 145-0064, Japan*
[b] *Tohoku National Fisheries Research Institute, Fisheries Research Agency, Shiogama, Miyagi 985-0001, Japan*
[c] *National Institute of Polar Research, Kaga, Tokyo 173-8515, Japan*
[d] *Tokyo University of Agriculture, Okhotsk, Abashiri, Hokkaido 099-2493, Japan*

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Abstract

We investigated the morphological features, vertical sinking fluxes, and number densities of the resting cells of ice-associated microorganisms in the 20–100 μm fraction of natural marine sediments collected from ice-covered and ice-free areas around Syowa Station, Lützow-Holm Bay, East Antarctica. We identified the resting cells of various taxonomic groups, including the spores of a diatom, cysts of three dinoflagellates, cysts of five oligotrich ciliates, and the eggs of a mesozooplankton. This is the first report of oligotrich ciliate cysts from Antarctic waters. The resting spores of *Thalassiosira australis* (diatom), cysts of *Polarella glacialis* (dinoflagellate), and egg type 1 sink to the bottom sediment during summer. Our results suggest that some planktonic and ice-associated microorganisms in Antarctic coastal areas send their resting cells to the bottom sediments as seed populations for the following generation.

Keywords: Resting spore; Resting cyst; Microorganisms; Antarctica; Marine sediment

1. Introduction

Many microorganisms in temperate and subarctic coastal waters produce resting cells that reside in sediment to survive unfavorable seasons; the germination of such cells initiates blooms (Sandgren, 1983; Dale, 1983; Garrison, 1984; Kim and Taniguchi, 1997; Marcus and Boero, 1998). In Antarctic marine ecosystems, various autotrophic and heterotrophic microorganisms inhabit brine pockets within sea ice and waters beneath the ice (Palmisano and Garrison, 1993; Garrison et al., 2005; Ichinomiya et al., 2007). Several microorganisms produce resting cells, including diatom resting spores (Syvertsen, 1985; Fryxell, 1989; Crosta et al., 1997; Ferrario et al., 1998), dinoflagellate and chrysophyte resting cysts (Buck et al., 1992; Marret and de Vernal, 1997; Stoecker et al., 1997; Harland et al., 1998), and crustacean zooplankton resting eggs (Ward and Shreeve, 1998; Swadling et al., 2004); however, little is known about the abundance and sinking fluxes of these resting cells in Antarctic coastal waters.

In the waters around Syowa Station, Lützow-Holm Bay, East Antarctica, ice algal populations develop within or immediately beneath fast ice in spring (Hoshiai, 1981; Watanabe and Satoh, 1987), and phytoplankton blooms have been observed in the underlying waters in summer (Ishikawa et al., 2001; Ichinomiya et al.,

* Corresponding author.
E-mail address: ichinomiya@lasc.co.jp (M. Ichinomiya).

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2007). Despite these observations, resting cells have received little attention in this area (Takahashi et al., 1986).

In the present study, we investigated the morphological features, abundance, and sinking fluxes through the water column of resting cells in sediments beneath fast ice near Syowa Station in the summer of 2005/2006. For comparison, we also sampled sediment from ice-free Nishino-Ura Cove to the west of Syowa Station. Based on these data, we discuss possible life histories of the microorganisms that produce benthic seed populations in coastal Antarctica. This paper also reports on the first papulifères identified in Antarctic waters. Papulifères are the cysts of oligotrich ciliates that possess a plug or papula in the extruding hole (Reid and John, 1983) and are commonly reported from coastal areas of the world oceans except for the Southern Ocean (Kim and Taniguchi, 1995; Montagnes et al., 2002; Agatha et al., 2005).

2. Materials and methods

Sediments were sampled on five occasions at Station A (St. A; 69°00′S, 39°37′E), to the north of Syowa Station, at a water depth of 67 m beneath fast ice (~1.8 m thick) between 29 December 2005 and 27 January 2006 (Ichinomiya et al., 2007). A sample was also collected from ice-free Nishino-Ura Cove (69°00′S, 39°35′E), to the west of Syowa Station, at a water depth of 8 m on 30 January 2006. Sediments were sampled using an Ekman grab sampler, and the uppermost *ca.* 1 cm was collected using a spatula. In the laboratory, a 5 g aliquot of the sediment was fixed with *ca.* 50 ml of filtered seawater with 2% glutaraldehyde. The sediments from St. A and Nishino-Ura Cove were dominated by the <63 μm (47%) and 250–500 μm (34%) grain-size fractions, respectively, corresponding to very fine sand and medium sand.

The fixed sediment samples were sonicated for 30 s, and the 20–100 μm fraction was sieved off and made up to exactly 100 ml with distilled water. Precisely 1 ml of the suspension was then placed on a counting slide to identify and count the resting cells using an inverted microscope. This procedure was repeated to observe whole 100 ml sediment suspension. Papulifères, easily identified by their yellowish-green fluorescence under blue excitation light after glutaraldehyde fixation (Ichinomiya et al., 2004), were counted under an inverted epifluorescence microscope. The size of each resting cell was measured with reference to an ocular micrometer.

Sinking cells were collected every 3–8 days from 29 December 2005 to 30 January 2006 using a cylindrical sediment trap moored at 20 m water depth at St. A. The sediment trap was 53 cm in length and 14.5 cm in inner diameter, with six sampling bottles located in the 27.5 cm^2 collecting area at the bottom of the trap. The trap was initially filled with artificial seawater with a salinity of *ca.* 35 $g\,l^{-1}$, without poison or fixative. At the time of sample retrieval, the seawater in the upper part of the sampling bottles was gently removed and the trapped sample in each one of the sampling bottles was transferred to a 500 ml polyethylene bottle. The sample was made up to 500 ml with filtered seawater with 2% formalin. In measuring the sinking flux of the obtained resting cells, 50–500 ml aliquots of the sediment trap samples were examined following the method of Utermöhl (1958), without sonication or sieving.

3. Results

3.1. Resting spores of diatoms

Sediments collected at both sites contained the resting spores of *Thalassiosira australis* Peragallo (average cell length (pervalvar axis), 19.0 μm; average diameter, 39.2 μm), endogenous-type spores wholly enclosed within the parent cell frustules (Syvertsen, 1985) (Fig. 1a; Table 1). The number densities of resting spores in the surface sediments at St. A showed a gradual increase over time from 3.4 cells g^{-1} (wet sediment) on 29 December to 14.8 cells g^{-1} on 27 January; the density at Nishino-Ura Cove on 30 January was 16.8 cells g^{-1} (Table 2). The sinking flux of resting spores was recorded only at St. A over the period from 4 to 30 January, ranging from 6.8×10^2 to 7.1×10^6 cells $m^{-2}\,d^{-1}$ (Table 3).

3.2. Resting cysts of dinoflagellates

Three types of dinoflagellate cysts were found in the sediments: those of *Polarella glacialis* Montresor, Procaccani & Stoecker, *Protoperidinium* sp. cf. *conicum*, and an unidentified species (Dinocyst type 1) (Fig. 1b–d). The cysts of *P. glacialis* were 15.5 μm long and 12.3 μm wide, prolate–spherical in shape, and covered in numerous recurved spines (Fig. 1b; Table 1), as described by Montresor et al. (1999). Because these cysts were smaller than the mesh size of the sieve, they were not counted although they were commonly found in the sediments at both sites. The sinking flux of *P. glacialis* cysts at St. A varied from 2.8×10^2 to 7.7×10^3 cells $m^{-2}\,d^{-1}$ over the course of the study period (Table 3).

Reniform cysts covered with numerous straight spines were also found (Fig. 1c), being larger than *P. glacialis* cysts (80.3 μm long and 51.0 μm wide; Table 1) and with similar morphology to that of *Protoperidinium conicum* (Wall and Dale, 1968). We therefore identified these cysts as *Protoperidinium* sp. cf. *conicum*. The

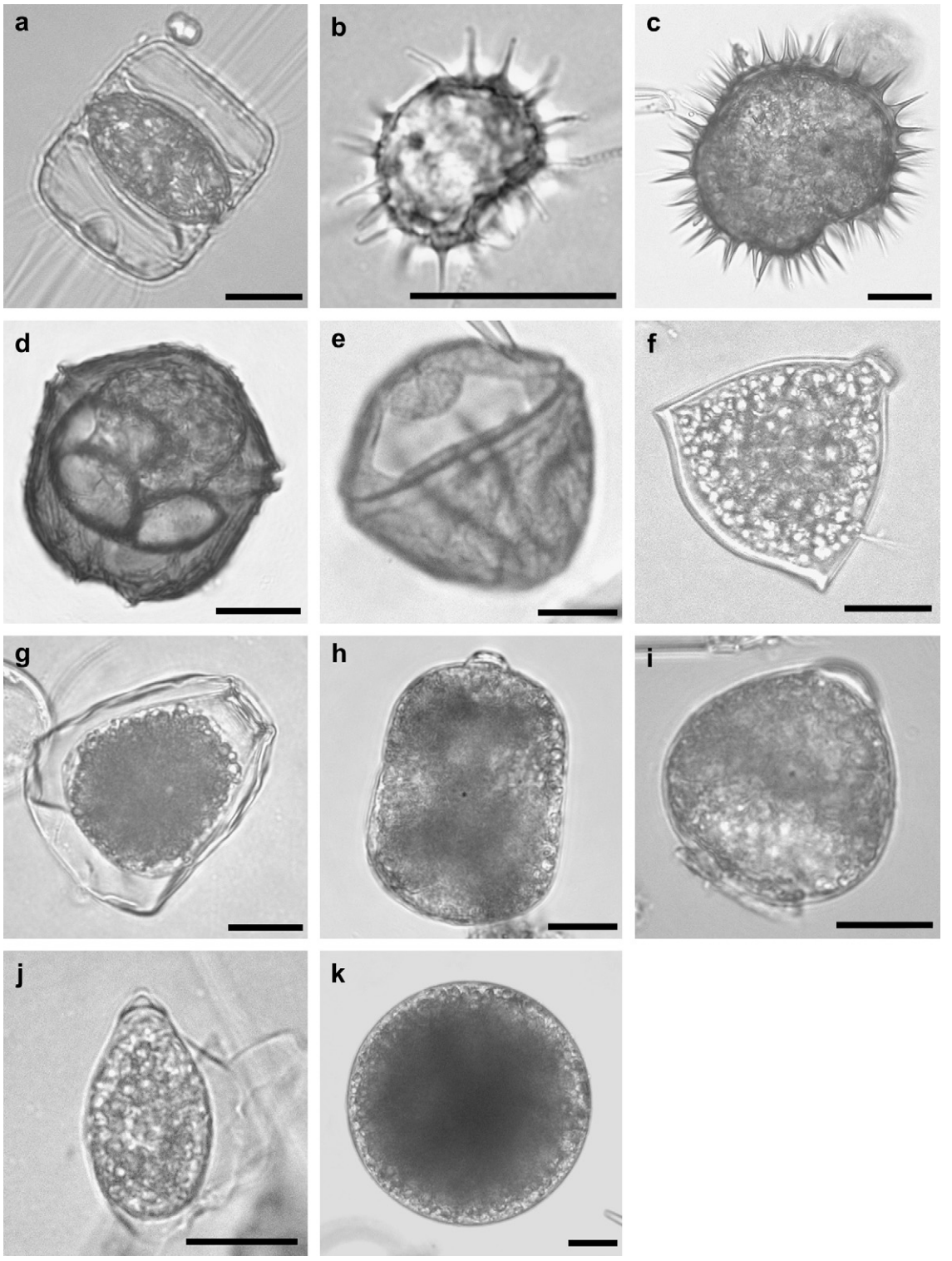

Fig. 1. Microphotographs of the resting cells of microorganisms in marine sediments collected around Syowa Station, Antarctica; (a): a resting spore of *Thalassiosira australis*; (b): a resting cyst of *Polarella glacialis*; (c): a *Protoperidinium* sp. cf. *conicum* cyst; (d): an intact cell of Dinocyst type 1; (e): an empty cell of Dinocyst type 1; (f): papulifère type 1; (g): papulifère type 2; (h): papulifère type 3; (i): papulifère type 4; (j): papulifère type 5; and (k): egg type 1, probably of a mesozooplankton. Scale bars = 20 μm.

Table 1
Size of the resting cells of microorganisms in the marine sediments collected around Syowa Station, Antarctica

Species or types	Size (SD, μm)		Number (*n*)
	Length	Width	
Diatom			
Thalassiosira australis	39.2 (7.5) (diameter)	19.0 (4.7) (pervalvar axis)	50
Dinoflagellates			
Polarella glacialis	15.5 (1.9)	12.3 (1.6)	50
Protoperidinium sp. cf. *conicum*	80.3 (1.5)	51.0 (1.0)	4
Dinocyst type 1	63.8 (5.3)	55.0 (0.7)	3
Oligotrich ciliates			
Papulifère type 1	56.6 (5.9)	53.1 (6.8)	11
Papulifère type 2	53.1 (6.9)	42.7 (4.4)	7
Papulifère type 3	71.4 (5.0)	51.0 (3.5)	13
Papulifère type 4	43.9 (3.9)	43.6 (3.4)	21
Papulifère type 5	37.0 (5.3)	22.7 (2.1)	3
Mesozooplankton			
Egg type 1	94.4 (3.1)		31

abundance of these cysts was very low: 0.4 cells g^{-1}, just above the detection limit of <0.2 cells g^{-1} (Table 2). They were recorded only on 18 and 27 January at St. A and were not found in the sediment trap samples.

Dinocyst type 1 had a pentagonal peridinioid morphology (Wall and Dale, 1968; Fig. 1d), and its empty shell possessed a hexagonal archeopyle (excluding hole; Fig. 1e). Intact cells were found only on 29 December at St. A (0.4 cells g^{-1}), although empty shells were always found (average 3.9 cells g^{-1}; Table 2).

3.3. Papulifères of ciliates

Five morphologically different types of papulifère were found (Fig. 1f–j): all enveloped with hyaline shells with no projections. Papulifère type 1 was trigonal with sharp basic angles, possessed a papula at the vertex, and was 56.6 μm long and 53.1 μm wide (Fig. 1f); type 2 was elliptical, covered with a fragile membrane, and was 53.1 μm long and 42.7 μm wide (Fig. 1g); type 3 was cylindrical, and the largest of those observed (71.4 μm long and 51.0 μm wide; Fig. 1h); and types 4 and 5 were elliptical, with the former being larger (43.9 μm, 43.6 μm; Fig. 1i) than the latter (37.0 μm, 22.7 μm; Fig. 1j).

The number densities of all five papulifères were similar at St. A, ranging from 0.2 to 0.5 cells g^{-1} on average (Table 2), but type 4 was by far the most abundant (28.8 cells g^{-1}) at Nishino-Ura Cove. No sinking cells were caught.

3.4. Mesozooplankton eggs

Spherical eggs of probably mesozooplankton origin (94.4 μm in diameter) were found in sediments from both sites (Fig. 1k). Their number densities were generally low (<0.2–3.4 eggs g^{-1}) at both sites, but reached 47.8 eggs g^{-1} at St. A on 4 January (Table 2). Sinking eggs were trapped between 29 December and 18 January (from 5.5×10^2 to 1.2×10^3 eggs m^{-2} d^{-1}; Table 3).

4. Discussion

We identified various types of resting cells and eggs of microorganisms in the 20–100 μm sediment fraction collected from ice-covered St. A and ice-free Nishino-Ura Cove, near Syowa Station (Fig. 1a–k). These findings indicate that some microorganisms have benthic seed populations in Antarctic coastal areas, as in temperate and subarctic waters. The resting cysts of many small organisms (<20 μm) such as chrysophytes and nano dinoflagellates have been reported previously

Table 2
Densities of the resting cells of microorganisms in sediments collected at St. A and Nishino-Ura Cove, close to Syowa Station

Resting cells	Density (cells g^{-1} of wet sediment)						
	St. A						Nishino-Ura
	29 Dec.	4 Jan.	10 Jan.	18 Jan.	27 Jan.	Average	30 Jan.
Thalassiosira australis resting spore	3.4	5.8	6.4	7.6	14.8	7.6	16.8
Protoperidinium sp. cf. *conicum* cyst	–	–	–	0.4	0.4	0.4	–
Dinocyst type 1							
Intact cyst	0.4	–	–	–	–	0.4	–
Empty cyst	1.4	3.8	7.2	4.0	3.0	3.9	–
Papulifère type 1	1.0	0.4	0.2	–	0.4	0.5	0.2
Papulifère type 2	–	0.2	–	–	0.2	0.2	0.2
Papulifère type 3	0.2	0.6	0.4	0.8	0.4	0.5	4.2
Papulifère type 4	–	0.2	0.2	0.2	–	0.2	28.8
Papulifère type 5	–	–	0.4	–	–	0.4	0.2
Egg type 1	0.4	47.8	–	0.2	–	16.1	3.4

Table 3
Sinking fluxes of the resting cells of microorganisms at St. A, north of Syowa Station, Antarctica

Resting cells	Sinking flux (cells $m^{-2} d^{-1}$)				
	29 Dec–4 Jan.	4–10 Jan.	10–18 Jan.	18–27 Jan.	27–30 Jan.
Thalassiosira australis resting spore	–	6.8×10^2	1.8×10^6	7.1×10^6	2.4×10^5
Polarella glacialis cyst	2.8×10^2	1.5×10^3	4.8×10^3	7.7×10^3	5.1×10^3
Egg type 1	5.5×10^2	5.5×10^2	1.2×10^3	–	–

from sea ice near Syowa Station and elsewhere around Antarctica (Takahashi et al., 1986; Buck et al., 1992; Stoecker et al., 1997). Such organisms may also have benthic seed populations in this area; however, their small size made it difficult to distinguish their cysts from abundant sediment particles in the present study.

Among the collected resting cells, the resting spores of *T. australis* were the most common (Tables 2 and 3). This species has been recognized as an ice-associated species in the Southern Ocean (Johansen and Fryxell, 1985; Fryxell, 1989; McMinn, 2000; Ishikawa et al., 2001; Scott and Thomas, 2005). Their number density in the sediment at St. A showed a gradual increase during the study period. The fact that several resting spores existed in the sediment at St. A on 29 December, before the newly formed spores started sinking from 4 January, suggests that the resting spores overwinter in the sediment. Because the germination of resting spores is activated by a certain degree of irradiance (McQuoid and Hobson, 1996) and the resting spores in the sediments beneath the ice are barely resuspended into the euphotic layer, they are not exposed to sufficient light to stimulate germination. It is therefore possible that they do not act as a seed population in areas with permanent ice cover; however, resuspension could occur in seasonally ice-free areas such as Nishino-Ura Cove, where resting spore formation of diatoms would be an effective survival strategy.

P. glacialis is an autotrophic dinoflagellate and a typical ice-associated species (McMinn and Scott, 2005), growing and sexually reproducing (cyst formation) in brine pockets within sea ice (Stoecker et al., 1992; Thomson et al., 2006). The cysts found in the sediments and the sediment trap at St. A would therefore have originated from sea ice (Table 2). Stoecker et al. (1998) hypothesized that cysts deposited on the bottom germinate in the sediment, and that the germinated vegetative cells become incorporated into the sea ice population. Our observations indicate that *P. glacialis* utilize not only sea ice but also bottom sediments for the storage of seed populations (Table 3).

To the best of our knowledge, the present discovery of papulifères in Antarctic waters is new to science, and papulifère types 1–3 are also new findings (Fig. 1f–j). We are unable to identify these new papulifères to the species level since morphological observation of planktonic vegetative cell is essential for species identification of papulifères (Kim, 1995). But they probably belong to *Strombidium* or a closely related genus, as with most papulifères (Reid, 1987; Kim, 1995; Kim and Taniguchi, 1995; Müller, 1996; Kim et al., 2002; Agatha et al., 2005). Such genera are commonly found in sea ice and plankton in Antarctic waters (Garrison and Gowing, 1993; Garrison et al., 2005; Wickham and Berninger, 2007). Our findings demonstrate that they also form benthic seed populations, along with diatoms and dinoflagellates, in Antarctic waters.

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